

REGENERATION IN AN EARTHWORM, *EISENIA FOETIDA* (SAVIGNY) 1826. II. POSTERIOR REGENERATION

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This contribution is the second in a series presenting the results of an attempt to obtain, for one particular species of earthworm, complete characterization of regenerative capacity with reference to exact levels. In this part, posterior regeneration, and by anterior substrates only, is considered.

SUMMARY OF PREVIOUS WORK

The information hitherto available as to posterior regeneration by anterior substrates of *E. foetida*, is summarized in Table II. Morgan once referred to one posterior regenerate, a monstrosity, as "a double tail." Other posterior regenerates of various workers from Morgan (1895) to Moment (1946) were not definitely characterized as to morphological nature. Even after rediscovery of anterior heteromorphosis in 1898-99 (see part I) no possibility of posterior heteromorphosis seems to have been anticipated. Very little evidence is available that might indicate morphological nature of many regenerates and the most useful clue, number of segments, may be of little value in certain circumstances.

The uncertainty as to nature of regenerates, paucity of data at most of those levels where operations were made, and lack of data for so many other levels, indicated need for a systematic investigation of regeneration at each level.

MATERIAL, METHODS AND NOMENCLATURE

In addition to the information in corresponding sections of part I, only a few comments are necessary.

Especial effort was made to avoid use of animals that had undergone amputation followed by enteroparietal healing without regeneration (see Gates, 1949b).

Previous work on other species had shown that accumulation of ingested material, such as earth or manure, which could not be passed out by the operated animal, frequently resulted in rupture. Regenerates of survivors were always deformed. To obviate those abnormalities and the higher mortality, as well as effects of pressure of accumulations on the regenerating region of worms which did not rupture, operated animals were at first kept in filter paper or paper towelling. Fibres of such materials were, however, ingested by some individuals in amounts sufficient to result in rupture. This always proved fatal, in *E. foetida*, within 48 hours. A fine grade of cheesecloth was then used. Edges of the cloth had to be hemmed so that free ends of threads were not exposed, as experience with that material, as well as with coarse towelling, showed that worms were able to pull

TABLE II
Posterior regeneration in Eisenia foetida

Level	Number of regenerates				Number of segments in regenerates	Comments on		Time days*	Author	Date	Page
	H	U	T	O		substrate	regenerate				
3/4				5				-6	Michel	1898	261
4/5				5				-6	Michel	1898	261
5/6				5				-6	Michel	1898	261
6/7	(1?)			5	+			-6	Korschelt	1898	79
7/8	(1?)			5	+			-6	Korschelt	1898	261
8/9	(1?)			5	+			-6	Michel	1898	261
9/10	(1?)				(7)			?	Korschelt	1898	79
10/11						6s + "3 angeschnittenen segmenten" See note		?	Korschelt	1898	80
11/12		1			0	(a)	Bud	20	Korschelt	1897	100
12/13				5				-6	Michel	1898	261
13/14				5				30	Morgan	1895	458
12/13+?	(1?)			5		12 + "einigen verletzten segmenten"		-6	Michel	1898	261
14/15					4			?	Korschelt	1897	100
15/16				5				40	Morgan	1895	458
16/17				15				60	Morgan	1897	571
17/18				4				?	Morgan	1895	458
18/19				1				7	Hescheler	1896	234
19/20				1				7	Hescheler	1896	234
				5				-6	Michel	1898	261
				1				7	Hescheler	1896	234
				3				40	Morgan	1895	458
				1				7	Hescheler	1896	234
				3				60	Morgan	1906	469
				1				7	Hescheler	1896	234
				22				110	Morgan	1897	571
20/21		1	3	1	28? ? ?		"Knob"				
				27			See note (b) "long posterior ends"				
21/22			1		15			49	Liebmann	1943	600-1
22/23			1		22 "abn"			?	Korschelt	1898	80
				3				60	Morgan	1906	465
								120	Morgan	1895	458

TABLE II—Continued

Level	Number of regenerates				Number of segments in regenerates	Comments on		Time days*	Author	Date	Page								
	H	U	T	O		substrate	regenerate												
23/24	{		2	1	"17-20 abn," 18	See notes (c) and (d). Mature Immature (age?) regenerated completely	"a half inch" "with double tail"	60	Morgan	1895	458								
			1	5				60	Morgan	1906	465-9								
24/25	{	4	15	3+, 12+, ca. 40	See notes (c) and (d). Mature Immature (age?) regenerated completely			"a half inch" "with double tail"	90	Morgan	1895	458							
		1	2						110	Morgan	1897	571							
25/26	{		1	1					50	See notes (c) and (d). Mature Immature (age?) regenerated completely	"a half inch" "with double tail"	60	Morgan	1906	465				
			1	?								10	Korschelt	1896	58				
			?									60	Morgan	1906	465				
												30	Liebmann	1942	378				
26/27	{	2	6	23, ca. 30					See notes (c) and (d). Mature Immature (age?) regenerated completely			"a half inch" "with double tail"	?	Morgan	1895	458			
			1											60	Morgan	1906	465		
28/29	{	maj.	min.	2									20-30 mm.	See notes (c) and (d). Mature Immature (age?) regenerated completely	"a half inch" "with double tail"	30	Morgan	1895	458
30/31																2	25	Liebmann	1943
31/32						72	Morgan										1906	463	
32/33						1	Morgan										1906	463-73	
33/34					3	Morgan	1906	463-73											
34/35					3	Morgan	1906	463-73											
35/36					1	Morgan	1906	463											
36/37					1	Morgan	1906	473											
37/38					1	Morgan	1906	463											
38/39					1	Morgan	1906	464											
40/41	7	Moment	1946	496															
50/51	180	Moment	1946	496															
60/61	19	Moment	1946	496															
70/71	31	Moment	1946	496															
80/81	118	Moment	1946	496															
-L 20S	{		5	6-7-9-15-19 6-7-13-17-20	See note (i)	Same regenerates two weeks later	26	Michel	1898	260									
							40	Michel	1898	260									
-L 10S	{		4	5-5-6-7 "a few segments" 3-4-4-5-6			26	Michel	1898	260									
?			Morgan				1906	471											
5			Michel				1898	260											

off and swallow lint in sufficient quantity to result in rupture of posterior end of substrate or the regenerate.

Use of starved or starving animals, in addition to reducing mortality, also provided greater uniformity in experimental conditions, for, if food was available, anterior substrates, having mouths, often did eat, while posterior substrates from the very same animals, having no mouths, could not eat.

Anterior substrate refers to any "cephalized" portion of the body, regardless of size, comprising the buccal region and extending back to a single posterior transection.

SUMMARY OF RESULTS

Healing in some individuals was enteroparietal rather than cicatricial. Such specimens did not regenerate in the two or three months before experiments were

NOTES TO TABLE II

H—Cephalic
U—Uncertain
T—Caudal

O—None
S—Segments

* Time may indicate day of death of last specimen, of last observations, or of termination of experiment. In case of Morgan's experiments time is approximate—because of infrequency and irregularity of examination of operated animals, and method of presentation of data.

(a) The cut was diagonal and from the data provided in the text as quoted above, level of regeneration, in accordance with previous practice (see Part I, Table I, note c), should be taken as 9/10. However, Figure 8 shows a substrate of at least 7, possibly 8, complete segments and major portions of two others (missing portions apparently not regenerated). Level of regeneration, according to the figure, should, perhaps, be taken as 10/11.

The figure does not have, in the seven-segment regenerate, the terminal notch that indicates, in certain other regenerates on the same page, presence of an anus.

In *Regeneration and Transplantation* (1907, p. 80, fig. 50B) the same substrate appears to have been reproduced but the regenerate, again without a terminal notch, is marked off into eight divisions, the last of which could represent a segment or a prostomium. Alongside (in Fig. 50A) is shown a substrate of 11 presumably complete segments with a regenerate of nine segments of which the terminal is notched (1927, p. 332, Fig. 188). If 50A is a representation of an actual specimen, caudal regeneration anterior to 20/21 is indicated.

(b) Figure C (Morgan, 1901, p. 8), shows a 20-segment substrate with a regenerate of 28 segments. Although 20/21 is the anteriormost level of regeneration definitely recorded by Morgan, two statements seem to indicate regeneration further forward.—"Anterior ends containing from thirteen (?) to thirty segments sometimes regenerate posteriorly" (summary, 1897, p. 584), and "as I have shown elsewhere, the power of regenerating a posterior end ceases rather suddenly about the level of the 15th segment" (1906, p. 463). In both, reference presumably was to a doubtful case of regeneration (posterior) at 13/14 by a two-surfaced fragment and not an anterior substrate. Note also "no cases of survival of as few segments as fifteen were ever found" (1895, p. 458).

(c) Number of segments in substrate, according to text, 25 or 24, according to table (I, p. 571), 24. The latter is taken as correct as Figure 1 shows 24 segments in the substrate.

(d) Figure 1 (Morgan, 1897) shows a regenerate with numerous metameric abnormalities, bifurcated distally, one bifurcation represented as having an anus. This is the posterior regenerate that was morphologically characterized.

(e) "The majority die after regenerating short pieces" at least some of which may well have been cephalic. "Those which survive do reform full size individuals."

(f) At EL 34/35 eight regenerates: abn., 19 (abn), 31, 37, 36-40 (abn), 40 (abn), 55 (abn), 61. Time, ca. 60 days. Actual level of regeneration could have been from 31/32-38/39.

(g) Morgan (1906) experimented in two regions behind 40/41; at the "middle" of the body (EL 50/51) and after excision of L25-20S (EL 75/76-80/81). Actual levels, when deter-

terminated (but see note (h), Table II). In other specimens a small bud was formed. At certain anterior levels, the bud shortly ceased to grow. At more posterior levels, further growth often enabled recognition of a growth zone producing segments by the rapid ventral or terminal methods (see Gates, 1948). In the former case, the ventral method eventually gave way to the terminal and finally the growth zone was reduced to a very small anal region, as in normal worms. Thereafter new segments were formed by the slow terminal method of normal, late-juvenile or post-juvenile growth. Regardless of length of time animals were kept after operation the regenerate always remained recognizable as such and clearly distinguishable from substrate.

Posterior regeneration, at levels behind 40/41, was obtained throughout the entire year.

A. After a single cut

Anterior substrates of 15 or fewer segments did not regenerate and in many cases probably did not live long enough to do so. At levels 16/17–19/20 small buds were formed but soon ceased to grow. These buds were still unpigmented, metamERICALLY undifferentiated and without terminal sculpturing 80–90 days after operation when experiments had to be terminated. The external appearance of such regenerates was more like that of a cephalic than a caudal bud.

Regenerates (metamerically organized growths) were obtained at each inter-segmental level from 20/21 posteriorly. In the Cambridge experiments percentage of regeneration gradually increased from 20/21, with 100% regeneration on substrates having transections at levels 32/33–39/40. With but two exceptions, all regenerates were caudal.

mined, were at 41/42–64/65 and 64/65–88/89. "In order to compare the rate of regeneration at the beginning and toward the end of its period of growth some of the same lot of worms that gave the records of Table IV were kept alive for another month (Jan. 6 to April 6) in order to see how much further the regeneration of new segments would continue. The results are given in the following Table IX" (1906, p. 473). But the worms of Table IX were "Cut behind girdle" as proved by number of segments, "at middle" and near posterior end, while none of the worms in Table IV were cut near the posterior end nor behind the girdle. Accordingly the comparable results were those of the two sets of regenerates at EL 50/51. Omitting from consideration those substrates in which segment number was not determined, the results appear to be as follows.—Two months; four substrates of 41, 47, 55, and 56 segments with regenerates respectively of 58, 44, 43, and 39 segments, average number of segments 46. Three months; seven substrates of 41, 48, 51, 51, 52, 53, and 59 segments with regenerates respectively of 53, 52, 46, 40, 36, 42, and 32 segments, average number of segments 43.

(h) Morgan's Table I (1897, p. 571) seems to indicate that regeneration at levels 20/21 and 24/25 began only in the second month after operation. (Also see second paragraph on p. 582.) Korschelt, however, obtained an unsegmented bud at 10/11 in 20 days and mentioned similar "Knospen" on other substrates presumably of the same series. Hescheler (1896, p. 242) found that the anterior half of an autotomized specimen of *Allolobophora chlorotica* (Savigny) 1826, regenerated only after nine months (autotomy in November, regeneration in August).

Liebmann (1942) apparently found no effect of season on posterior regeneration in *E. foetida* though other species failed to regenerate in winter months. In 31 October operations at 12/13–26/27 (Morgan, 1895, p. 458) no regeneration was obtained, while in 8 January operations at 19/20–27/28 one regenerate was secured. No data available as to season of Morgan's 1897 operations and Korschelt's 1898 operations. Korschelt's bud at 10/11 was obtained in August.

(i)—L20S Level of cut when last twenty segments were excised.

In the first exceptional case the small regenerate, produced in 65 days at 32/33, had the external characteristics of an inverted buccal segment, the prostomium ventral rather than dorsal. The second exceptional regenerate, produced at 34/35 in 65 days, was differentiated into six segments of which the proximal five were normally setigerous. The terminal segment had all the external characteristics of a normal buccal segment with normal prostomium.

At each level from 92/93 to 124/125 one, two, three, or ten segments were removed. Every specimen (100+) regenerated. Regenerates produced after removal of ten segments were hypomeric, as at levels anterior to 92/93. After removal of one to three segments, regenerates were usually equimeric or hypermeric. In one specimen, number of segments in regenerate and substrate totalled 126, one more than the maximum hitherto recorded for the species.

Attempts at removal of a portion only of the so-called anal segment also resulted in hypermeric regeneration.

B. After a previous regeneration

Attempts to test for effects of previous regeneration were made in several series. In E13 and E14, the first two and three segments were removed and the substrates were allowed to regenerate for 14 days, at which time the worms were depositing faecal pellets of paper indicating that the digestive system was functional. Two days later posterior portions were removed at 8/9 or 15/16 (all anterior regenerates equimeric). All substrates of eight segments died without regeneration. Three fifteen-segment substrates survived until preservation 65–95 days later. Each had a regenerate at 15/16. One was abnormal. The second, though two mm., long, was metamerically undifferentiated and with the terminal portion sculptured into the shape of an inverted buccal segment as in the exceptional regenerate at 32/33. The other regenerate was marked off into four segments but setae were unrecognizable externally and the terminal portion was unsculptured (no indication of prostomial demarcation, buccal or anal invagination).

In E43 the anteriormost eight segments were removed. Six worms survived this operation. Forty-five days after the first operation, posterior portions were removed at 35/36. Three survivors of the second operation regenerated in the time available. No differences were noted between those regenerates and others produced at 35/36 by substrates that had not previously regenerated.

C. After starvation

Worms that had been starved seemed to regenerate as well as those which had not been starved prior to operation. As a result of several months starvation the chloragogue layer on the gut of substrates was drastically reduced. The masses of coelomic corpuscles which had been readily visible in young tail regenerates of animals operated upon shortly after collection, were not noted in those regenerating after weeks of starvation.

DISCUSSION

A zero level posteriorly for tail regeneration apparently has been indicated by Liebmann (slightly to left of c, 1943, p. 601) and by Moment (at 90/91, by extra-

polation in curve of Fig. 2, 1946, p. 406). New results presented above show there is no zero level posteriorly.

Liebmann and Moment apparently also found that production of new segments ceased at or shortly after the first month. The author's results agree with those of Michel (1898) and some of Morgan (1895-1906), in showing that production of segments may be continued longer than a month. After reduction of the regenerative growth zone to the small anal region characteristic of the normal adult, further segment formation apparently is continued by a slow terminal method.

Establishment in tail regenerates, at the same level and in the same experimental conditions, of different types of growth zone (ventral, large or small terminal, see Gates, 1948), with different capacities for segment formation, suggests that the variation may be due to the condition of the operated animals (note also considerable variation in number of segments regenerated at each of Moment's levels, 1946, p. 496).

In favorable conditions, and at levels from 40/41 backwards, season apparently has no influence on ability to regenerate posteriorly (by anterior substrates) in *E. foetida*, although seasonal inability to regenerate posteriorly has been reported from other Lumbricid species by Liebmann (1942, for *Lumbricus terrestris*)¹ and by Abeloos and Avel (1928, for *Allolobophora longa* and *A. terrestris*). Effect of season on posterior regeneration at levels in front of 40/41, in *E. foetida* as well as other Lumbricids, remains to be determined (see note h, Table II).

The hypomery of tail regenerates at anterior levels and after removal of ten or more segments posteriorly, in the author's experiments, is in accord with D'Arcy Thompson's rule "that regeneration tends to fall somewhat short of a *complete* restoration of the lost part; a certain percentage only of the lost tissues is restored" (1942, p. 274). Equimery and hypermery at levels behind 92/93, when three or fewer segments were removed, provide, in earthworms, a second exception to the rule.² Michel (1898) had a single case of hypermery after removal of five segments (see Table II), but no information is available to indicate that the specimen was normal and complete at time of amputation. Moment (1946) obtained some hypermery in tail regenerates at 50/51 and 80/81, apparently mostly from specimens with only 80-89 segments, possibly also in some with 90-99 segments. As number of segments in juveniles 7.5 + mm. long may be 85-115 (Gates, 1948), and usually is somewhat over one hundred by six months (Liebmann, 1943, p. 600), Moment's worms with the smaller numbers of segments, 80-89 or even 90-99, may have been amputees, possibly with enteroparietal healing and no regeneration (see Gates, 1949b).

Posterior heteromorphosis, i.e., regeneration of a head at the posterior surface of an anterior substrate, hitherto has been unrecognized in the Lumbricidae. Such heteromorphosis has, however, already been recorded from species of two other families of earthworms, in the Glossoscolecoid *Criodrilus lacuum* by Janda (1926) and in the Megascolecoid *Perionyx excavatus* by Gates (1927). In that respect, at least, pattern of regenerative capacity now appears to be similar in the three families.

¹ There are no valid records of posterior regeneration by this species in any season!

² The first exception; equimery of anterior regenerates in the anteriormost portion of the axis (see part I).

Posterior heteromorphosis having been recognized in *E. foetida*, it is now possible to suggest cases in which similar results may have been obtained by previous investigators, though unrecognized. Among such cases may be mentioned: the "majority" of Liebmann's animals operated at 30/31 which died "after regenerating short pieces," and Korschelt's regenerates at 12/13 (+ ?), 9/10 (or 10/11), 8/9, 7/8 and 6/7 (see Table II). In fact, the only evidence available to indicate that posterior regenerates in *E. foetida*, at levels anterior to 20/21, are other than cephalic, is Korschelt's figure (1907, Fig. 50A, see note (a), Table II) of a specimen about which nothing else is known. In spite, then, of the failure of the present and some other authors to obtain any regeneration anterior to 20/21, there appears to be a possibility of heteromorphosis as far forwards as 6/7. This is supported, to some extent, by the heteromorphic heads regenerated by reversed grafts³ in three different Lumbricid species: *E. foetida* (Hazen, 1899), *Allolobophora longa* (Ruttloff, 1908, and Leyboldt, 1910), and *A. caliginosa* (Crowell, 1937).

Cases of heteromorphosis from reversed grafts have all been at rather anterior levels, 7/8 (Hazen and Ruttloff), region of 8/9-7/8 (Leyboldt), 12/13 (Crowell). Levels of heteromorphosis, involving a single transection only, were somewhat more posterior. The level for Janda's case, in *C. lacuum*, was 22/23. The level for *P. excavatus* was not published, but almost certainly was in front of 20/21 and probably behind 12/13. Formation of heteromorphic structures in *E. foetida*, as far back as 34/35, accordingly had not been anticipated, though expected in a more anterior region where no regeneration (except uncounted, inhibited buds) was obtained by the author.

Regeneration of heteromorphic heads at levels 6/7, 9/10, 32/33, 34/35, etc., is believed to indicate similar regenerative ability at all of the intermediate levels.

Number of segments in heteromorphic heads on reversed grafts usually has been small for the level: 2 segments at 7/8 (Hazen), 3 in region of 8/9-7/8 (Leyboldt), 3, 4, and 5 at 7/8 (Ruttloff), unrecorded for Crowell's regenerates. However, Janda's regenerate, following simple transection only, at 22/23, had 16 segments, and Korschelt's at 9/10 had seven segments. Homomorphic head regenerates may have 16 segments in *C. lacuum* and nine segments (the maximum hitherto recorded for the Lumbricidae) in *E. foetida* (see part I). It would not be surprising if further work demonstrates an ability to produce at any particular level, in the proper conditions, as many segments in heteromorphic as in homomorphic head regenerates.

Regeneration of a heteromorphic head at 34/35 where a homomorphic tail may also be regenerated, indicates for *E. foetida* a region of bipotential regenerative capacity for posterior regeneration, such as has already been demonstrated in part I for anterior regeneration. For the present the posterior limit of the region is placed at 34/35 by the regenerate just mentioned above. The anterior limit is placed at 20/21 by the foremost recorded level of homomorphic regeneration. The region of bipotential capacity for anterior regeneration, as delimited in part I, is between 35/36

³ At levels anterior to 20/21, regenerates from reversed grafts have usually been heads which must be considered heteromorphic with reference to original orientation of cut surfaces. The single exception was a regenerate that "erwies sich bei mikroskopischer Untersuchung als Hinterregenerat" (Ruttloff, 1908, p. 471), at 7/8 in *L. terrestris*. This case (Ruttloff's No. 60), is also of especial interest because of lack of valid records of tail regeneration by *L. terrestris* from ungrafted substrates.

and 18/19. The two regions are so nearly coextensive as to suggest possibility of identity.

Regeneration of heteromorphic heads anterior to 20/21, and regeneration of such heads behind 20/21, is not in accord with the polarization of the head aggregate and the specificity of the eleocytic aggregates postulated by Liebmann (1943).

SUMMARY

Anterior substrates of *E. foetida*, cut exactly at intersegmental furrows, regenerated homomorphic tails at levels from 20/21 back, with no zero level posteriorly. Regenerates were hypomeric, except posteriorly and after removal of three or fewer segments, and then were equimeric or hypermeric. Heteromorphic heads, previously unrecognized in the Lumbricidae, were obtained at 34/35, 32/33, 15/16 (but only after a previous anterior regeneration). Head-like buds were formed at 16/17–19/20.

Starvation and season did not inhibit homomorphic regeneration at levels behind 40/41.

Posterior regenerative capacity in a region from 34/35 to 20/21 is characterized as bipotential, as a posterior regenerate in that region may be a homomorphic tail or a heteromorphic head.

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